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Published in:
Agriculture, Ecosystems and Environment

DOI:
10.1016/j.agee.2018.06.029

Print publication: 01/10/2018

Document Version
Peer reviewed version

A meta-analysis on the effects of climate change on the yield and quality of European pastures

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Abstract

As has been widely reported, climate change will be felt throughout Europe, though effects are likely to vary dramatically across European regions. While all areas are expected to experience elevated atmospheric CO_2 concentrations (↑C) and higher temperatures (↑T), the north east will get considerably wetter (↑W) while the south much drier (↓W). It is likely that these changes will have an impact on pastures and consequently on grazing livestock. This study aims to evaluate the expected changes to pasture yield and quality caused by ↑C, ↑T, ↑W and ↓W across the different European regions and across different plant functional groups (PFGs). Data was collected from 143 studies giving a total of 998 observations. Mixed models were used to estimate expected changes in above ground dry weight (AGDW) and nitrogen (N) concentrations and were implemented using Markov Chain Monte Carlo simulations. The results showed an increase in AGDW under $\uparrow$C, particularly for shrubs (+71.6%), though this is likely to be accompanied by a reduction in N concentrations (-4.8%). $\uparrow$T will increase yields in Alpine and northern areas (+82.6%), though other regions will experience little change or else decreases. $\uparrow$T will also reduce N concentrations, especially for shrubs (-13.6%) and forbs (-18.5%). $\downarrow$W will decrease AGDW for all regions and PFGs, though will increase N concentrations (+11.7%). Under $\uparrow$W there was a 33.8% increase in AGDW. While there is a need for further research to get a more complete picture of future pasture conditions, this analysis provides a general overview of expected changes and thus can help European farmers prepare to adapt their systems to meet the challenges presented by a changing climate.

Key words: Climate change, meta-analysis, pastures, above ground dry weight

1. Introduction

Depending on global emissions, global average atmospheric CO_2 concentrations are expected to rise to between 421 and 936 ppm by 2100 (IPCC, 2013). Under a mid-range emissions scenario (IPCC representative concentration pathway (RCP) 4.5), Europe can expect average annual temperature increases of between 1 and 4.5°C, with the greatest warming in the south in summer and in the north-east in winter (EEA, 2017). Annual precipitation is predicted to increase for northern and large parts of continental Europe (up to 25% increase under RCP4.5), while decreasing in southern Europe (up to 25% reduction under RCP4.5) (Jacob et al., 2014). Extreme events (heat-waves, heavy precipitation events and droughts) will all become more common across the continent (Kovats et al., 2014).

A great deal is already known about how specific plant species respond to specific climatic changes in specific ecosystems. However, it is useful to generalise this knowledge to a wider scale in order to make appropriate management and policy decisions. Changes in pasture yield and quality will have knock-on effects on the livestock production sector and it is important for farmers, policy makers and researchers to know what to expect.

Elevated atmospheric CO_2 levels (↑C) generally increase plant yields, though results are conflicting when considering the relative responses of different plant functional groups (PFGs) (Ainsworth and Long, 2004; Nowak et al., 2004; Wang et al., 2012). In terms of plant quality, Dumont et al. (2015) found that ↑C decreases forage nitrogen (N) content, though to varying extents for different geographic areas.

The effect of increasing air temperatures (↑T) on plant growth is closely related to water availability. In mid to high latitudes and in mountainous regions, it is predicted that ↑T will increase plant production (Dumont et al., 2015; Hopkins and Del Prado, 2007; Watson et al., 1997); this is partly due to the longer growing season (Kipling et al., 2016; Trnka et al., 2011). However, Alpine regions have been observed to be vulnerable to droughts (Schmid et al., 2011), which would have a negative effect on growth, making it hard to know what the overall impact will be. Northern Europe will experience increased water availability (↑W), which promotes plant growth and has a positive effect on plant quality (Matías et al., 2011; Sardans and Peñuelas, 2013).

Southern Europe, by contrast, is expected to experience decreased forage production when climate change impacts alone are considered (up to 30% reduction by 2050 in Portugal and southern France) due to a combination of drought and very high temperatures (Dumont et al., 2015; Rötter and Höhn, 2015), although it is not clear what the net result will be when combined with the fertilisation effect of ↑C. Meta-analyses have shown that warming and drought tend to reduce nutrient availability in plants, particularly in terms of N content, though again there is regional variation (Lee et al. 2017; Dumont et al. 2015).

Given the expected geographic variation in the effects of climate change on pastures, it is useful to consider these effects on a regional basis. It is also helpful to consider the effects on different PFGs, as these could lead to changes in pasture composition. In this study we use a meta-analysis to quantify the effects of ↑C, ↑T, ↑W and ↓W on both the yield and quality of pasture and forage species across five European regions. We also investigate the impacts on yield and quality for different PFGs and consider the effects of multiple simultaneous climatic changes.

2. Methods

The search for studies for this meta-analysis was conducted in January 2017 using the Web of Science database. Additional studies were taken from grey literature, previous meta-analyses on a similar topic, bibliographies of key review articles, expert consultation and internet searches (see Supplementary Material A for full details of the search terms used). Only studies written in English were used due to limitations on resources; no limits were set on the publication date. To be included, a study had to meet the following criteria:

- Conducted in Europe, or else in controlled laboratory conditions;
- Includes at least one desirable forage species commonly found in Europe;
- Assesses the effect of $\uparrow$C, $\uparrow$T, $\uparrow$W or $\downarrow$W on plant life;
- Provides quantitative data on changes in plant yield or quality, including mean, standard deviation (SD) (or equivalent) and sample size.

Where plants were sampled several times over a period, only data from the final sampling was used. Several studies compared different cultivars or genotypes of the same species; these were taken as replicates. For the purposes of the present study, plants were grouped into shrubs, forbs, legumes and graminoids. The vast majority of plant species included in the analysis were perennial types with a C3 photosynthetic pathway. Some studies did not report the precise mix of plant species used so it is possible that some C4 species were present; these were treated as ‘mixed species’ experiments. Each study was assigned to one of five geographical regions: Alpine, Atlantic, continental, northern and southern (see figure 1). Laboratory studies were assigned a region based on the climatic conditions applied and the plant species used.

In total, 143 studies were used in this meta-analysis (see Supplementary Material B and C for full details), providing 998 observations (one observation is counted as a value under climate change conditions together with the associated control value). Eighty-two studies investigated the effects of ↑C, with an average increase of 284 ± 79 ppm (mean ± SD) (number of observations *n* = 476) over an average period of 475 days; 45 studies looked at the effects of ↑T, with an average increase of 3.2 ± 1.7°C (*n* = 301) over an average of 418 days; 59 studies looked at the effects of reduced water availability (↓W), with an average water reduction of 79 ± 26% compared with control treatments (*n* = 357) over an average of 70 days (mainly in summer); 9 studies considered the impact of increased water availability (↑W), with an average water increase of 117 ± 96% (*n* = 48) over an average of 189 days (around half during summer, with others during winter and spring). Of these studies, 32 considered the effects of multiple simultaneous climatic changes (162 observations). This CO_2 increase was in the middle of the predicted range for 2100 atmospheric concentrations and the temperature increase also falls within the expected range. The ↑W and ↓W treatments were both quite extreme but are over much shorter time periods than the ↑C and ↑T treatments; they could be seen to represent a particularly wet or dry season.

The natural logarithm of the response ratio (L) was used to estimate the effect of the different climate treatments, where $L_i = ln(\bar{X}_{Ti}/\bar{X}_{Ci})$ ($\bar{X}_{Ti}$ and $\bar{X}_{Ci}$ are the mean outcomes for experiment i under test and control conditions respectively). Assuming $\bar{X}_{Ti}$ and $\bar{X}_{Ci}$ are normally distributed, the variance of L_i (S_i) can be approximated as:

$$S_i = \frac{(SD_{Ti})^2}{n_{Ti}\bar{X}_{Ti}^2} + \frac{(SD_{Ci})^2}{n_{Ci}\bar{X}_{Ci}^2}$$

(Hedges et al., 1999)

where SD_{Ti} and SD_{Ci} are the standard deviations and n_{Ti} and n_{Ci} are the sample sizes of experiment i under test and control conditions.

Mixed models were used in most cases, with fixed effects relating to plant type, climatic treatment, management practices and experimental methodology and with the individual studies as a random effect. Fixed effects models were used for yield under ↑T and ↑W since in these cases the random effect of the individual studies was found to be insignificant (using a likelihood ratio test). The choice of fixed effects was determined through REML analysis in GenStat 16th Ed. (VSNi, 2013) and the model was implemented in WinBUGS 1.4.3 (MRC, 2007).

The model can be described as follows:

$$L_i \sim N\left(\theta_i, S_i^2\right)$$

with

$$\theta_i \sim N(\mu, \tau^2)$$

where θ_i is the true mean of L_i; μ denotes true overall effect across all studies and τ^2 is the between-study variance. To incorporate fixed effects, μ is generalised to a regression function:

$$\mu = \beta_0 + \beta_1 Q_1 + \beta_2 Q_2 + \cdots + \beta_p Q_p + \alpha_0 R$$

where $Q_1, \ldots, Q_p$ represent *p* fixed effects (e.g. fertiliser use, treatment time, European region, etc.) and *R* represents the random effect. Since this models the natural logarithm of the response ratio, the overall effect μ was converted to percentage change using the following equation:

$$Percentage\ change = e^{\mu} - 1$$

WinBUGS fits Bayesian models using Markov Chain Monte Carlo (MCMC) simulations. Non-informative priors were used and all observations were weighted according to their variance. The model was run with three chains to check sensitivity to different initial conditions. Fifty-thousand iterations were sufficient to ensure convergence for all models, with the first 1,000 discarded as burn-in. Bias and homogeneity of the studies was assessed by means of funnel plots. The goodness-of-fit of the models was assessed using posterior predictive p-values (Meng, 1994) and by comparing the cumulative frequency distributions of predicted and observed data (Ntzoufras, 2009).

Analyses were performed looking at the effects of ↑C, ↑T, ↓W and ↑W on plant above ground dry weight (AGDW) and on above ground N concentration for different plant functional groups (PFGs) across the five European regions. Studies which looked at multiple simultaneous climatic treatments were used to assess the effects of the different combinations. Where region or PFG was not a significant factor (or when there were only a small number of observations available), then their results are grouped. Analyses were only run when data from at least five different studies was available. This had the effect that the only plant quality measure used was N concentration.

3. Results

3.1 Bias and sensitivity analysis

In all cases, the models were found to have an acceptable fit. The observed cumulative frequency distribution fell within the 95% credible interval of the predicted cumulative frequency distribution in almost all cases. For some models (N concentration under ↓W and both AGDW and N concentration for different combinations of treatments), a few points were just outside the interval at the upper end of the distribution, suggesting that these models slightly over-predict results at the upper extreme. Posterior predictive p-values ranged from 0.487 to 0.537 across all models.

Funnel plots were made for each analysis (examples in figure 2). The plots shown here are representative of all plots, with those for AGDW generally not showing signs of bias but indicating considerable heterogeneity between studies. Exceptions were plots for forbs under ↓W conditions and the continental region under ↑T, where higher standard errors of measurement were associated with greater negative response to the climatic change. Funnel plots for N concentration generally revealed bias and also high levels of heterogeneity. The plot for N concentration under ↑C was biased towards a greater negative response. For ↓W the overall effect was positive though the bias was towards a reduced or even negative response. For all PFGs except legumes under ↑T the effect was negative and the bias was towards a reduced or positive response; for legumes the bias was towards a more negative response.

3.2 Above ground dry weight

Shrubs exhibit a considerably higher growth increase than other PFGs under ↑C (+71.6% growth increase), with forbs, legumes and graminoids being more similar in their responses (figure 3). Graminoids are less likely to experience elevated growth under ↑C than legumes or forbs (with the chances of increased growth being 55.7%, 94.6% and 96.9% respectively, calculated from the posterior distribution) and generally exhibit less growth than legumes, which in turn exhibit less growth than forbs (mean increases of +0.6%, +8.5% and +13.0% for graminoids, legumes and forbs respectively).

Shrubs and legumes both experience significant yield reductions under ↓W (-33.8% and -31.8% respectively). Forbs, and graminoids are both likely to have decreased yields (84.8% and 91.5% likelihoods respectively), with mean decreases of -10.7% and -11.9%. There were no significant differences between PFGs under ↑T and insufficient data for ↑W.

Changes in AGDW for different European regions under ↑T and ↓W are shown in figure 4. The southern region is missing for ↑T due to a lack of available data and the northern region is missing for ↓W as this is not an expected consequence of climate change. ↑T increases growth in Alpine and northern areas (+82.6%) and reduces it in the continental region (-32.6%). There is negligible effect on plant yield in the Atlantic region. Under ↓W, there is a significant decrease in AGDW in the continental region (-42.2%) and likely decreases everywhere else, (the likelihoods of a reduction are 87.4%, 95.9% and 84.9% for the Alpine, Atlantic and southern regions respectively). For ↑W, all the data came from the Alpine, continental and northern regions, which are all areas which are predicted to receive increased rainfall under climate change, at least for part of the year. AGDW increases under ↑W (+57.1%), though with a large credible interval (17.2 – 110.4%), possibly due to the small dataset and the wide regional variation; unfortunately there was insufficient data for a regional division under ↑W. There were no significant regional differences for ↑C.

So far only single climatic changes have been considered (though data from experiments with multiple treatments was used, with the additional treatments included in the models as a fixed effect). The expected changes in AGDW under different combinations of climatic treatments are shown in figure 5. ↑C+↑T increases plant growth (+32.8%), while ↑T+↓W and ↑C+↑T+↓W are likely to lead to reductions. For ↑C+↓W, the two effects seem to cancel each other out, producing very little change in AGDW. Combining ↑W with ↑T is likely to increase growth (80.3% chance of an increase), though the credible interval is very large, which is likely a result of the small amount of data available for ↑W+↑T.

3.3 Nitrogen concentration

The expected changes in N concentration under ↑T for different PFGs are shown in figure 6. Shrubs and forbs both display significant reductions in N concentration (-13.6% and -18.5% reductions respectively), while N concentration in graminoids is likely to decrease (average reduction of -5.6% with a 94.3% chance of a decrease).

Neither PFG nor region had a significant effect for the other climatic changes and so overall average changes are shown (figure 7). Under ↓W there was a significant increase in N concentration (+11.7%), while it is likely to decrease under ↑C (-4.8% with a 84.8% chance of a decrease).

It is interesting to note, when comparing how N concentration changes for different combinations of climate treatments (figure 8), that ↓W produces little change in N concentration when considered alone, while in the previous analysis (figure 7) it produced an increase. This is because all treatments involving ↓W were included in figure 7, including e.g. ↑C+↓W, ↑T+↓W, etc. It appears that ↑C+↓W decreases N concentration (-12.8%) and ↑W increases it (11.8%), but other combinations produce a slight but non-significant reduction.

4. Discussion

The present study set out to quantify the effects of ↑C, ↑T, ↑W and ↓W on pasture yield and quality across Europe. The impacts of these changes on yield and quality for different PFGs were also assessed. The results presented above address these objectives.

4.1 Bias and sensitivity analysis

For all funnel plots there was a large degree of heterogeneity. This is to be expected given the differing methodologies, plant species, locations and soil types across the studies. At least some of this variability is accounted for in the analysis through the fixed and random effects. There are several possible explanations for the bias that was recorded. It may be that some categories (plant species, locations, etc.) are over-represented, there may be publication bias, or it may be that due to the small number of observations for some PFGS and regions that it is not possible to make an accurate estimate. For shrubs in particular there were only a small number of studies available and these results should be treated with caution.

Due to the bias found it may be that the results for N concentration under ↓W and ↑T should show a greater negative response and that those under ↑C should have a smaller response. The more extreme observations which have a large standard error should not have too great an influence as the observations were weighted according to their variance.

4.2 Above ground dry weight

Looking at the change in AGDW under ↑C (figure 3), the results show that shrubs exhibit a larger degree of growth than other PFGs. In this analysis, the average CO_2 increase for experiments involving shrubs was 184 ppm, whereas it was 290 ppm for all other PFGs, making this result particularly surprising. Ainsworth and Long (2004) had a similar finding for trees, but other studies (Nowak et al., 2004; Wang et al., 2012) found contrasting results. This is an area that would benefit from further independent studies.

When looking at ↓W, there was a greater reduction in AGDW for shrubs and legumes than for forbs and graminoids. Elst et al. (2017) suggest that grasses may be more resistant to drought than legumes due to their generally deeper rooting depth, giving them greater access to the limited water resources. The large reduction in shrub yield compared to graminoids could be attributed to competition effects, as proposed by Kreyling et al. (2008).

For ↑T the effect across functional groups was very similar, there being a slight increase in AGDW, although it should be noted that there were comparatively few studies looking at ↑T for southern Europe where high temperatures are expected to have especially negative effects, which could have skewed the results.

In general, it seems that in areas which are not water-limited, all functional groups will benefit to some extent, though particularly shrubs. An increase in shrub encroachment could have variable effects on pastures, some positive and some negative (Eldridge et al., 2011; Rivest et al., 2011). In water-limited areas it is harder to predict which functional groups will benefit the most when all climate change effects are considered, however given the variation in responses between groups it seems likely that there will be changes in pasture composition.

Looking at change in AGDW by region (figure 4), the increase in growth for the Alpine and northern regions under ↑T is unsurprising since these are areas which are often temperature-limited and which will benefit from longer growing seasons. The increased growth under ↑W conditions is also to be expected as it reduces the chance of growth being limited by lack of water, though water-logging may become an issue if the ↑W becomes too extreme. The results show a great deal of uncertainty about how large the growth might be; comparatively few studies were found which dealt with the effects of ↑W, making more precise estimates practically impossible. Given that annual precipitation is predicted to increase over a large part of northern and continental Europe, this is certainly an area worthy of further investigation. Under ↓W conditions it is interesting to note that a greater decrease in AGDW is predicted for the continental region than the southern, where droughts are expected to be more of a problem. This may be because plants in the southern region are already partially adapted to $\downarrow$W conditions (Pugnaire et al., 1999; Volaire et al., 2009).

When comparing the different combinations of climatic treatments (figure 5), the most interesting results are for $\uparrow$C+$\uparrow$T and $\uparrow$C+$\uparrow$T+$\downarrow$W, since these combinations most accurately represent future conditions (EEA, 2017). While $\uparrow$C+$\uparrow$T will cause yields to go up, adding in the effect of $\downarrow$W negates the positive growth response. It may be that irrigating pastures, particularly in southern and continental Europe, will become increasingly necessary as conditions become drier, though this will put an increased strain on diminishing water resources (EEA, 2017). It is unfortunate that no studies could be found looking at the effects of $\uparrow$C+$\uparrow$T+$\uparrow$W, since this would be useful for predicting future plant growth in northern Europe; however, given that both the $\uparrow$C and $\uparrow$T+$\uparrow$W results show a positive response in AGDW, it seems safe to assume that yields will increase in this region.

4.3 Nitrogen concentration

Looking at N concentration under $\uparrow$T, the general decreasing trend can be explained as a natural consequence of increased growth: as plants get bigger their N concentration becomes more diluted. The relatively minor reduction in legumes is likely due to an enhancement of N fixing caused by warming (Sardans et al., 2008;

Zavalloni et al., 2012). Different PFGs have also been found to allocate N in different ways as a response to warming, which could be having an effect here (Sardans et al., 2008). There may also be competition effects at play (most of these experiments were conducted on multi-species swards), as suggested by Andresen et al. (2009). With some PFGs showing higher growth increases and others showing lower reductions in N concentration under ↑T, it seems that swards containing multiple PFGs are better for livestock than those with only a single PFG, as they enable livestock to benefit from the higher yields while at the same time still having sufficient access to protein.

No regional differences were found for N concentration for any of the climatic treatments. The likely reduction under ↑C conditions has been widely documented and can be attributed to some combination of increased growth, changes in Rubisco activity (Leakey et al., 2009) and changes in N allocation (Cotrufo et al., 1998). The increase in N concentration under ↓W is likely due to the reduced growth and also to changes in allocation (Sardans et al., 2008).

Looking at combinations of climate treatments (figure 8), ↑C+↓W shows a clear decrease in N concentration, but other combinations exhibit very little change. This may be due to there being a lot of different factors in play which may be cancelling one another out (for example changes in growth, Rubisco activity, allocation and N uptake). It should also be noted that some of these treatment combinations only featured in a very small number of studies. Further research would provide a clearer picture of the likely outcomes of these combinations of climatic changes.

4.4 Impacts on livestock

Increases in AGDW are a positive result from a livestock perspective. Assuming grazing animals were not already at their maximum intake capacity then there is considerable scope to increase feed intake, leading to increased performance. Of course decreases in yields will have the opposite effect. In terms of forage quality, the general reduction in N concentration indicates decreased protein content, which can have a wide range of negative impacts on livestock (Landau et al., 2000; Schröder et al., 2003). It is likely that farmers will need to make increased use of concentrate feeds to compensate for the drop in protein. Irrigation may also become increasingly necessary (where feasible) to counteract the negative effects of droughts. Where irrigation is not possible, farmers may need to consider using different breeds or species, or else moving to other areas.

4.5 Other factors

Only three of the studies used involved grazing livestock on the study area. To get a realistic idea of the effects of climate change on forage, it would be useful if there was more data available for grazed plant-life, since the presence of livestock would also have an influence. There are also other factors which play a role; our analysis generally shows ↑W as having positive effects, but if the ↑W is the result of extreme rainfall events then the effect could be deleterious. Increases in ozone concentrations (Fuhrer, 2009; ICP Vegetation, 2011) and changes in the distribution and destructiveness of pests and pathogens (Bale et al., 2002; Jaggard et al., 2010) will also affect forage species. More research is needed to determine how all these different factors will interact in the future.

5. Conclusion

The present study highlights future trends in pasture yield and quality in different European regions. The general results of the meta-analysis can be used to inform farmers and policy makers around future land-use scenarios and animal management options.

$\uparrow$C increases AGDW, particularly for shrubs (+71.6%), though is likely to reduce N concentrations (-4.8%). $\uparrow$T will increase yields in Alpine and northern areas (+82.6%), though other regions will experience little change or else decreases. $\uparrow$T will also reduce N concentrations, especially for shrubs (-13.6%) and forbs (-18.5%). $\downarrow$W will decrease AGDW for all regions and PFGs, though will increase N concentrations (+11.7%). Under $\uparrow$W there was a 33.8% increase in AGDW.

In general, areas which will become warmer and wetter (in particular the northern region and parts of the Alpine and continental regions) can expect higher yields, though this will likely be accompanied by reductions in N concentration. Where conditions become warmer and drier (particularly southern Europe and parts of the continental region), there will be reductions in both yield and probably also N concentration. In areas where predicted climatic changes are less extreme (for example the Atlantic region), changes in pastures will be more moderate, though a reduction in N concentration is likely. How yields will be affected in such areas will largely depend on water availability.

Funding

This work was supported by the Horizon2020 SFS-01c-2015 project entitled "Innovation of sustainable sheep and goat production in Europe (iSAGE)" (grant number 679302). It was also partly supported by the Rural & Environment Science & Analytical Services Division of the Scottish Government.

Competing Interests

Conflicts of interest: None

Supplementary material

A: Search terms and sources used to find studies for the meta-analysis

B: Studies included in the meta-analysis

C: The regions, climatic treatments, yield and quality parameters, plant functional groups and methodologies used in each study

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Figures

Figure 1: Regional classification (Kovats et al., 2014)

Figure 2: Funnel plots for (a) above ground dry weight of graminoids under elevated atmospheric CO_2 concentration and (b) N concentration under elevated atmospheric CO_2 concentration. The x-axis shows the natural logarithm of the response ratio of results under climatically altered and control conditions. The dashed lines show pseudo 95% confidence limits and the dotted line indicates the overall effect estimate

Figure 3: Mean change in above ground dry weight (AGDW) under (a) elevated atmospheric CO_2 concentration and (b) reduced water availability, grouped by plant functional group. Error bars represent 95% credible intervals

Figure 4: Mean change in above ground dry weight (AGDW) under (a) elevated air temperature and (b) reduced water availability, grouped by region. Error bars represent 95% credible intervals

Figure 5: Mean change in above ground dry weight (AGDW) for different combinations of climate treatments, including elevated atmospheric CO_2 concentration (↑C), elevated air temperature (↑T), reduced water availability (↓W) and elevated water availability (↑W). Error bars represent 95% credible intervals

Figure 6: Mean change in N concentration under elevated air temperature, grouped by plant functional group. Error bars represent 95% credible intervals

Figure 7: Mean change in N concentration under elevated atmospheric CO_2 concentration (↑C) and reduced water availability (↓W). Error bars represent 95% credible intervals

Figure 8: Mean change in N concentration for different combinations of climate treatments, including elevated atmospheric CO_2 concentration (↑C), elevated air temperature (↑T), reduced water availability (↓W) and elevated water availability (↑W). Error bars represent 95% credible intervals

Figures

Figure 1

Figure 2

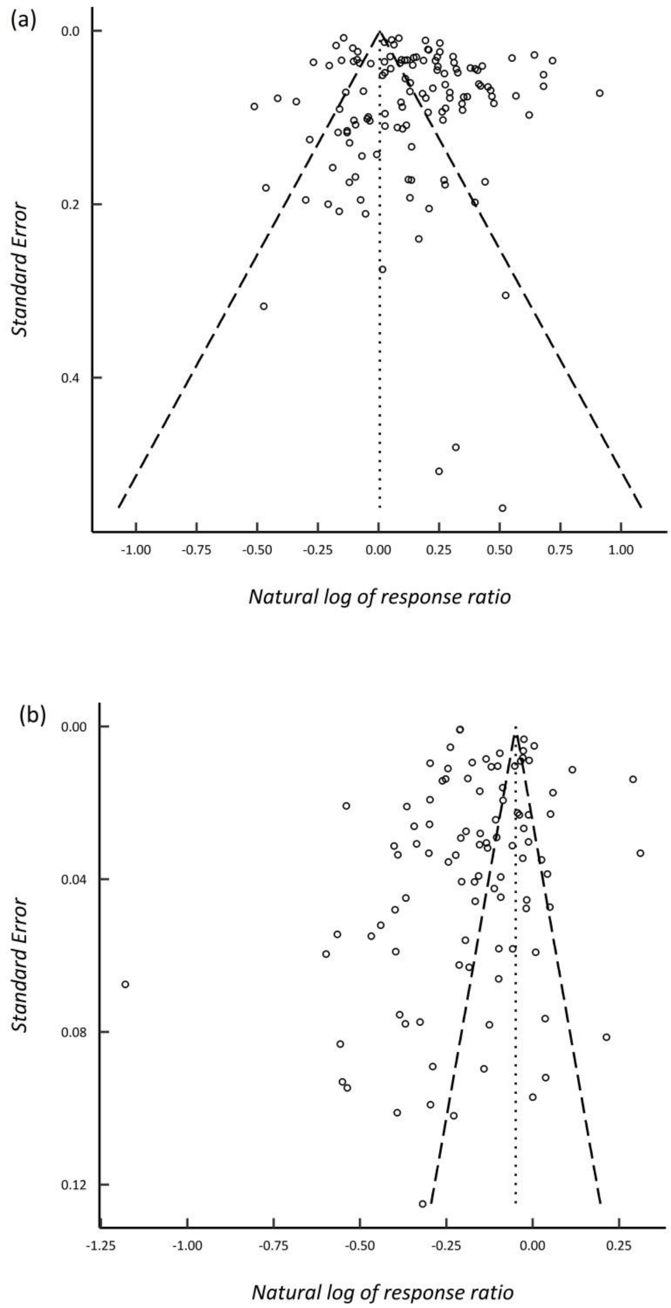

(a)
Standard Error
0.0
0.2
0.4
-1.00
-0.75
-0.50
-0.25
0.00
0.25
0.50
0.75
1.00
Natural log of response ratio
(b)
Standard Error
0.00
0.04
0.08
0.12
-1.25
-1.00
-0.75
-0.50
-0.25
0.00
0.25
Natural log of response ratio

Figure 3

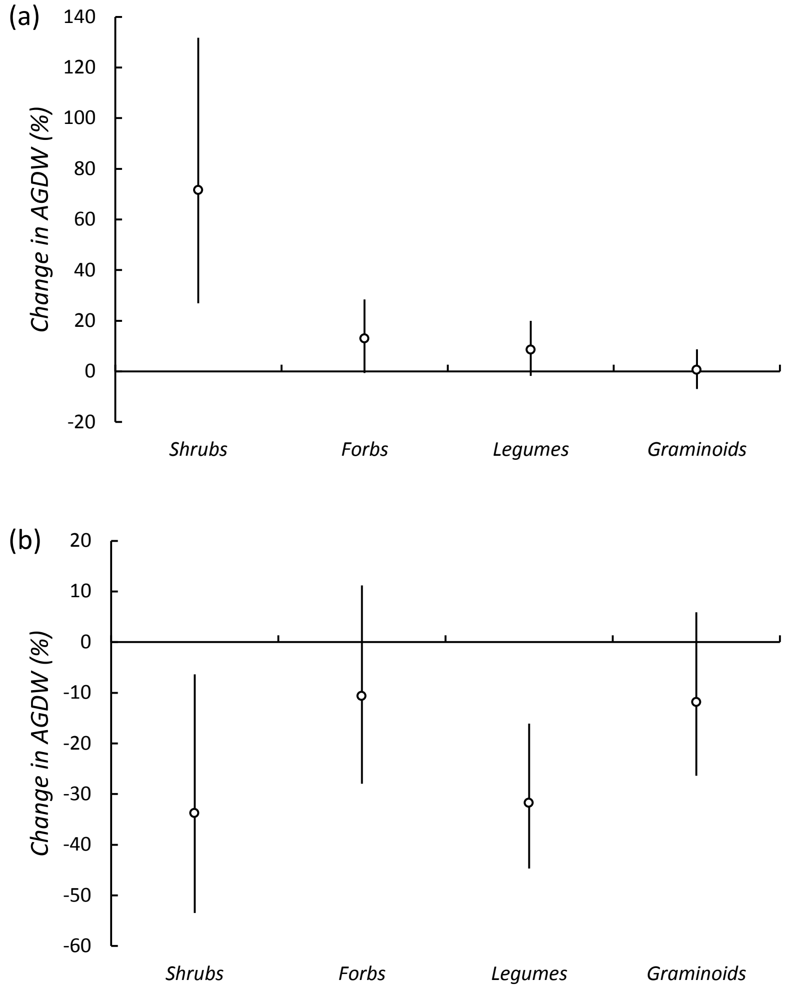
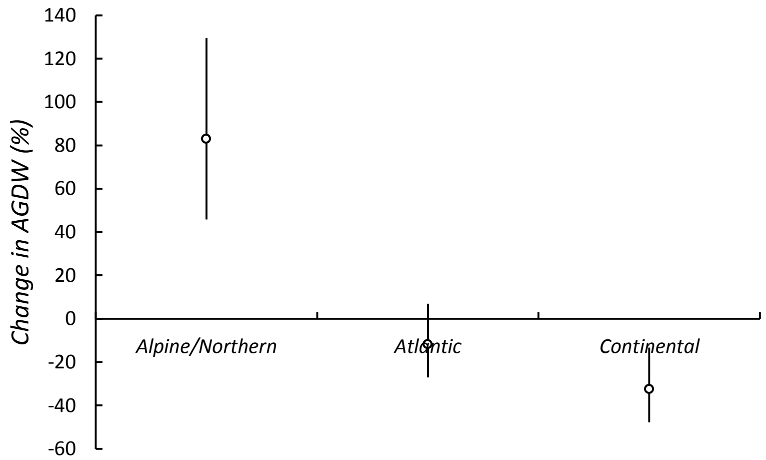

(a)
Change in AGDW (%)
140
120
100
80
60
40
20
0
-20
Shrubs
Forbs
Legumes
Graminoids
(b)
Change in AGDW (%)
20
10
0
-10
-20
-30
-40
-50
-60
Shrubs
Forbs
Legumes
Graminoids

Figure 4


Change in AGDW (%)
140
120
100
80
60
40
20
0
-20
-40
-60
Alpine/Northern
Atlantic
Continental

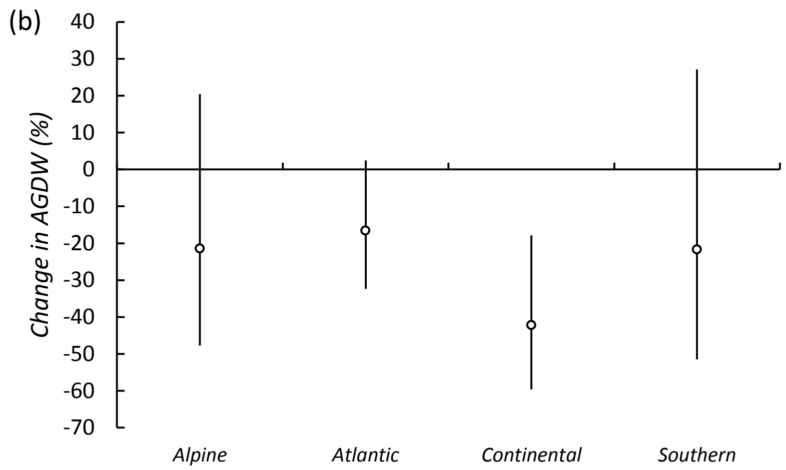


Figure 5

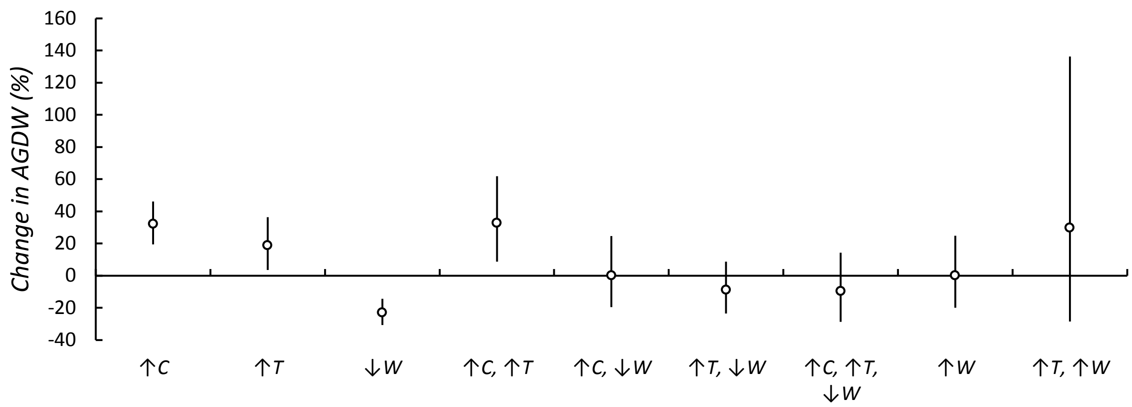


Figure 6

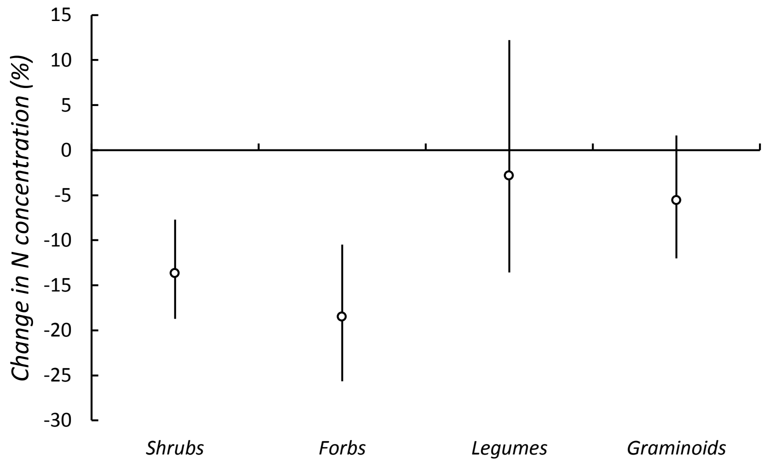
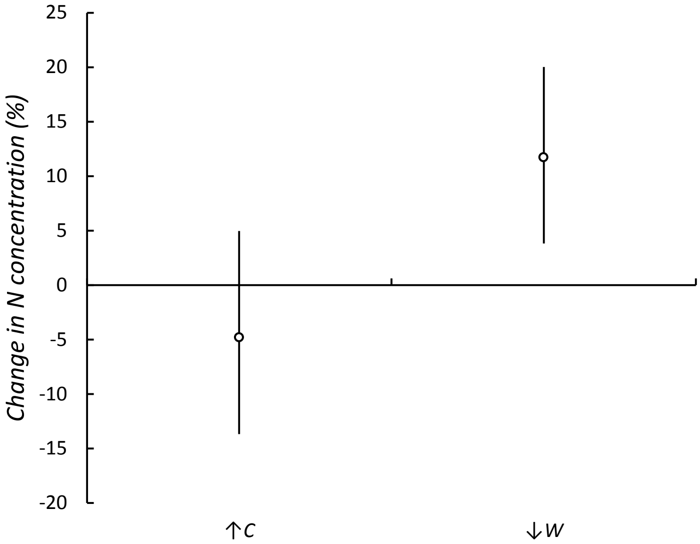
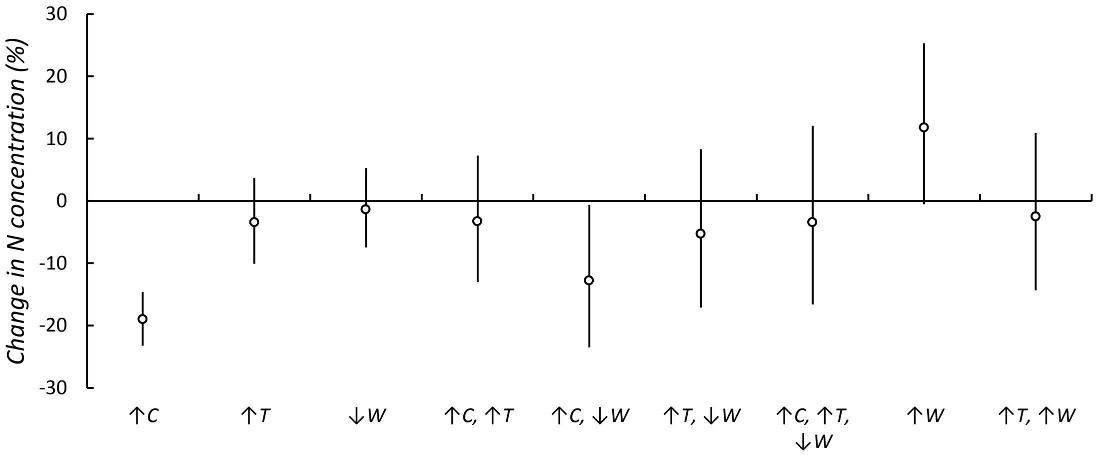


Figure 7


Change in N concentration (%)
25
20
15
10
5
0
-5
-10
-15
-20
↑*C*
↓*W*

8


Change in N concentration (%)
30
20
10
0
-10
-20
-30
↑*C*
↑*T*
↓*W*
↑*C*, ↑*T*
↑*C*, ↓*W*
↑*T*, ↓*W*
↑*C*, ↑*T*, ↓*W*
↑*W*
↑*T*, ↑*W*